

TAXONOMY OF *SERICOCARPUS* (ASTERACEAE: ASTEREAE)

Guy L. Nesom

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

Sericocarpus is returned to generic status as a North American endemic hypothesized to be more closely related to relatives of *Solidago* than to *Aster* (or any other white-rayed taxa), where its five species have most recently been included. A technical description of the genus, key to the species, and taxonomic summary of *Sericocarpus* are presented. One new combination is proposed: *Sericocarpus oregonensis* Nutt. var. *californicus* (Durand) Nesom.

KEY WORDS: *Sericocarpus*, *Aster*, *Gutierrezia*, Asteraceae, Astereae, Solidagininae

Sericocarpus Nees has long had a standing and relatively complete nomenclature as a separate genus (see below), surviving even the conglomeritic approaches of Bentham (1873) and Gray (1884) to the concept of *Aster*. It is the element most recently accreted to *Aster* (Cronquist 1947, 1955) as well as one of the most disparate among the American taxa in that genus, as it is now broadly conceived. Gray (1880) regarded *Aster* subg. *Biotia* as "nearly related to *Sericocarpus*," but he never formally merged the latter with *Aster*. Regarding its addition, Cronquist concluded the following (1947, p. 148): "If *Aster* is to be accepted in the extended sense, however, *Sericocarpus* must follow the other segregates to intra-generic rank. The only basis on which the several species of *Sericocarpus* might be distinguished generically is their narrow, relatively few-flowered heads." His comparisons of these features to species of *Aster* (sensu lato) noted similar variation scattered in various other species of the genus, mostly in the *Doellingeria*, *Eucephalus*, and *Biotia* groups, providing him with sufficient evidence to submerge *Sericocarpus*. Most recent treatments of *Sericocarpus* have followed Cronquist by including it within *Aster*. Fernald (1950) and Ferris (1960), however, maintained it as a distinct genus, though without comment. Jones (1980) treated *Sericocarpus* as a subgenus of *Aster*;

Sample & Brouillet (1980a) treated it as a separate section (informally) within subg. *Aster*.

Notwithstanding Cronquist's considerably more lengthy discussion, Torrey & Gray (1841, p. 109) came closest to providing the best rationale for placing *Sericocarpus* within *Aster*. With regard to *A. gracilis* Nutt., they noted that Nuttall [*Gen. N. Amer. Pl.* 2:158. 1818] "correctly remarked the alliance of this plant to *Aster spectabilis* [Ait.] on the one hand (some forms of which it greatly resembles), and to *Sericocarpus conyzoides* (Willd.) Nees [= *S. asteroides* (L.) B.S.P.] on the other: it almost connects the latter genus with *Aster*." Both *A. gracilis* and *A. spectabilis* are unequivocally members of subsect. *Spectabiles* A. Gray, a relatively primitive subgroup within North American *Aster*, and *A. gracilis* and *Sericocarpus* are indeed remarkably similar in their entire, evenly spaced leaves, turbinate-cylindric heads on short pedicels and contracted into a dense corymb, phyllary morphology, white rays, and dilated pappus apices. Critical features of *Sericocarpus*, however, place it with a group of primarily yellow-rayed genera closely related to *Solidago* L., although it certainly is one of the most primitive in the latter group. In my view, the parallel similarity between *A. gracilis* (and other *Spectabiles*) and *Sericocarpus* may reflect their common inheritance of genes from a not-too-distant ancestral matrix out of which the Solidagininae and a portion of North American *Aster* sensu lato arose (Nesom in prep.). The similarity of one of the species of *Sericocarpus* to *Solidago* was alluded to by Michaux in the epithet "solidagineus" (see below). Conversely, the *Aster*-like habit of another of the species was noted in one of the epithets applied to it.

The species of *Sericocarpus* are characterized most significantly by the following features: leaves punctate, sessile but not clasping, heads small, mostly cylindric, sessile and glomerate or nearly so, borne in a relatively compact, flat-topped capitulescence; phyllaries strongly graduated in length, strongly whitish-indurated and slightly keeled in all but the apex, the apex with a sharply demarcated green patch; ray flowers few, white, and relatively short; disc flowers mostly white with relatively long, recurved-coiling lobes; collecting appendages of the disc style branches merely papillate toward the apex, not spreading hairy from base to apex; achenes densely hairy, mostly turbinate; and pappus bristles distinctly dilated at the apex. In its combination of flat-topped capitulescence, punctate leaves, floral morphology, and morphology of the collecting appendages, it is more closely similar to genera of the subtribe Solidagininae (Nesom 1991b, 1993) than to any species of *Aster* or related, white-rayed genera. Among *Solidago* and its relatives, the sessile-glomerate heads, and the relatively small, sericeous achenes are further specializations shared particularly with the "*Gutierrezia* lineage." Within this group, the relationships of *Sericocarpus* apparently lie most closely with a heterogeneous group of $x=9$ genera centered primarily in the eastern United States, including the white-rayed *Gundlachia* A. Gray and the yellow-rayed *Chrysoma* Nutt.,

Euthamia (Nutt.) Nutt., and *Bigelovia* DC. (Nesom 1993).

If *Sericocarpus* produced yellow rays, its overall resemblance to the subtribe Solidagininae would have been more quickly recognized. White rays are unusual in this predominantly yellow-rayed group, but they are present not only in *Sericocarpus* but also occur in one species of *Solidago* L. as well as other taxa in the subtribe: in the Caribbean genus *Gundlachia*, one species of *Oligoneuron* Small (Nesom 1993), several species of *Gutierrezia* Lag., and one species of the western North American *Tonestus* A. Nels. (Nesom 1991a). The monotypic *Thurovia* Rose of the *Gutierrezia* lineage is rayless but produces distinctly white disc corollas.

The cladistic analysis by Jones & Young (1983) placed *Sericocarpus* within *Aster* subg. *Aster* (sensu Jones 1980 as well as Semple & Brouillet 1980a) as the sister taxon to the *Spectabiles* group; all of these in turn formed the sister group to sect. *Radulini*, sect. *Biotia*, and sect. *Integrifolii*, all also of subg. *Aster*. In their phenetic analysis, and in the "branch-swapping" cladogram based on the initial topology of their published phenogram, the position of *Sericocarpus* changed radically from the "Wagner analysis" cladogram they displayed. A visual inspection of the Jones & Young data (character state changes were not shown on their cladogram) suggests that whatever characters linked *Sericocarpus* to subg. *Aster* must be significantly homoplasious. Further, at least two significant morphological specializations for inferring monophyly in this part of the Astereae were not included in their scoring and analysis: foliar punctations, these sometimes with a sessile-glandular cap, and the nature of the collecting appendages of the disc flower style branches. Among North American taxa that Jones (1980) regarded as *Aster*, punctations are found only in *Sericocarpus* and two other species (*A. nemoralis* Ait. and *A. reticulatus* Pursh); they also occur in two Eurasian species groups sometimes included in *Aster*: *Linosyris* Cass. and *Galatella* DC. Jones & Young did not report any variability in style branch morphology other than the shape and relative length of the disc style appendages.

The placement of *Sericocarpus* within subg. *Aster* (Semple & Brouillet 1980a; Semple *et al.* 1983; Jones & Young 1983) first reflected the implicit assumption that the species indeed belonged in the genus *Aster*. The more specific placement of *Sericocarpus* (by Semple & Brouillet) then relied primarily on chromosome number and similarities in phyllary morphology between *Sericocarpus* and the species of their subsect. *Aster* (the latter mostly equal to the *Spectabiles* group sensu Jones 1980). In a related study emphasizing chromosomal data, however, Semple & Brouillet (1980b) noted that the NOR chromosomes of *Sericocarpus* differed in morphology from those in the rest of the species in their subg. *Aster*, having instead the NOR morphology hypothesized by them to be primitive for *Aster* (sensu lato). While the phyllary morphology of *Sericocarpus* is similar to some species of *Aster* (a distinctly demarcated, green apical patch, indurated below), similar morphology also

occurs in groups outside of *Aster*, including some genera of Solidagininae.

The five species of *Sericocarpus* are split in distribution between the eastern and western United States, but there does not appear to be any correlated morphological division. *Sericocarpus asteroides* stands apart from all the rest of the species in its prominently toothed, basally disposed leaves; *S. tortifolius* (Michx.) Nees is distinctive from the others in the prominent resin globules associated with the punctate glands and also its twisted leaves; *S. linifolius* is distinctive in its lack of vestiture and nearly linear leaves. All are species of open to dry woodlands and margins except *S. rigidus*, which occurs on prairies. *Sericocarpus rigidus* is relatively rare and its reproductive biology has been studied in detail (Clampitt 1987). The chromosome number is uniformly $n=9$ within the genus, with reports for all taxa except *S. rigidus* (Anderson *et al.* 1974; Huziwara 1965; Jones & Smogor 1984; Pinkava & Keil 1977; Semple 1985; Semple & Brouillet 1980b; and Semple *et al.* 1983, 1989). There is no evidence of hybridization among any of the species or between *Sericocarpus* and any other genus.

The species of *Sericocarpus* are well-characterized in many regional treatments, but the last complete treatment of the genus was more than a century ago (Gray 1884). A taxonomic account of *Sericocarpus*, with formal summaries of the species taxonomy, is provided here. The species names as currently found in most literature are marked with an asterisk.

Sericocarpus Nees, *Gen. Sp. Aster.* 148. 1832. LECTOTYPE (Britton & Brown 1913): *Sericocarpus solidagineus* (Michx.) Nees = *Sericocarpus linifolius* (L.) B.S.P. *Aster* subg. *Sericocarpus* (Nees) A.G. Jones, *Brittonia* 32:238. 1980. *Aster* sect. *Sericocarpus* (Nees) Semple, *Phytologia* 58:429. 1985.

Aster sect. *Serratifolii* G. Don, *Hort. Brit.* 347. 1830. LECTOTYPE (Sundberg & Jones 1987): *Aster conyzoides* Willd. = *Sericocarpus asteroides* (L.) B.S.P.

Aster sect. *Leucoma* Nutt., *J. Acad. Nat. Sci. Philadelphia* 7:82. 1834. LECTOTYPE (designated here): *Aster tortifolius* Michx.

Oligactis Rafin., *Fl. Tellur.* 2:44. 1836. Not *Oligactis* (Kunth) Cass. 1825. TYPE: *Sericocarpus asteroides* (L.) B.S.P.

Perennial herbs, with stems erect, mostly unbranched below the capitulescence, with simple or short-branched caudices, arising from a short to long, fibrous-rooted rhizome. Leaves mostly 1(-3)-nerved, entire or toothed, mostly cauline (basally disposed in *Sericocarpus asteroides*), epetiolate, not clasping, punctate, the punctae sometimes obscure. Heads small and mostly cylindric, commonly sessile in glomerules, borne in a relatively compact, flat-topped

capitulescence; phyllaries in numerous series, strongly graduated in length, strongly whitish-indurated (cartilaginous) and slightly keeled in all but the apex, the apex greenish, sometimes squarrose. Ray flowers mostly 3-8, the ligules white, not coiling or only slightly so upon maturity or drying; disc corollas pale yellow to whitish, sometimes becoming purple (mostly in *S. asteroides*), narrowly tubular-funneliform without an abrupt dilation, the lower portion of the tube sometimes becoming indurate at maturity, the lobes relatively long, lanceolate, recurved-coiling; style branches with linear-lanceolate collecting appendages, the collecting hairs long at the base, quickly reduced to papillae on the distal region of the appendages. Achenes obpyramidal (to obconic in *S. oregonensis* Nutt. and *S. tortifolius*), moderately to densely sericeous; pappus of numerous barbellate bristles in 2-3 equal to subequal series (1[-2] series in *S. linifolius*), those of at least the inner florets slightly but distinctly dilated at the apex.

KEY TO THE TAXA OF *SERICOCARPUS*

1. Leaves mostly basally disposed, the lower with prominently toothed margins, the cauline reduced upward, becoming entire, punctations obscure or apparently absent, widespread in the eastern U.S. *S. asteroides*
1. Leaves all cauline, not reduced upward, the margins entire (or sometimes with a distal pair of teeth in *S. tortifolius*), punctations distinct or not. (2)
 2. Leaves linear-oblong to linear-oblongate, the lamina glabrous, distinctly punctate; widespread in eastern U.S. *S. linifolius*
 2. Leaves elliptic to elliptic-obovate or oblanceolate, the lamina hairy, foliar punctations distinct to obscurely visible. (3)
3. Leaves densely dotted with minute resin globules associated with the punctate glands; phyllary surface puberulent; southeastern U.S. *S. tortifolius*
3. Leaves punctate mostly on the lower surface, sometimes obscurely so, without resin globules; phyllary surface glabrous; western U.S. (4)
 4. Plants mostly 1-3 dm tall; leaves 2.5-3.5 cm long, lower surface not distinctly reticulate-veined; heads usually in a single cluster; ray flowers (1-)2(-3) per head, ligules 1-3 mm long; Washington and Oregon. *S. rigidus*
 4. Plants mostly 4-12 dm tall; leaves 4-8 cm long, lower surface distinctly reticulate-veined; heads usually in several to many separate

- clusters; ray flowers (4-)5(-7) per head, ligules 4-7 mm long; Washington to California. *S. oregonensis* (5)
5. Leaves scabrous-puberulent; northcentral and northwest California to Washington. *S. oregonensis* var. *oregonensis*
5. Leaves densely hirsute or pilose; Sierra Nevada of western California. ...
..... *S. oregonensis* var. *californicus*
1. *Sericocarpus asteroides* (L.) B.S.P., *Prelimin. Cat. N.Y. Pl.* 26. 1888. Not O. Kuntze 1891. BASIONYM: *Conyza asteroides* L., *Sp. Pl.* 2:861. 1753. *Aster asteroides* (L.) MacMillan, *Metasperm. Minn. Valley* 524. 1892. Not *Aster asteroides* (Colla) Rusby 1893. *Aster marilandicus* Michx. [*nom. nov. illeg.*], *Fl. Bor.-amer.* 2:108. 1803. Based on *Conyza asteroides* L. *Aster conyzoides* Willd. [*nom. nov. illeg.*], *Sp. Pl.* 3:2043. 1803. Based on *Conyza asteroides* L. *Sericocarpus conyzoides* (Willd.) Nees [*nom. illeg.*], *Gen. Sp. Aster.* 150. 1832. **Aster paternus* Cronq. [*nom. nov. illeg.*], *Bull. Torrey Bot. Club* 74:149. 1947. Based on *Conyza asteroides* L.
- Sericocarpus asteroides* (L.) B.S.P. f. *albopapposus* Farwell, *Pap. Mich. Acad. Sci.* 1:100. 1923.
- Sericocarpus asteroides* (L.) B.S.P. f. *roseus* Svenson, *Rhodora* 30:136. 1928.
- Aster plantaginifolius* Nutt. ex Nees, *Gen. Sp. Aster.* 299. 1832.
- Aster leucanthemus* Rafin., *Med. Repos.* 2, 5:359. 1803.

As observed by Cronquist (1947), the names in *Aster* proposed by Michaux and Willdenow, based on *Conyza asteroides* but with an epithet in replacement of "asteroides," were illegitimate, because that epithet was unoccupied in *Aster* at the time. The much later combination *Aster asteroides* (L.) MacMillan, however, was valid and legitimate, obviating the necessity for another new name for this species. Cronquist (p. 148) noted only that "the name *Aster asteroides* is preoccupied" but provided no details of citation or authority. Unless there is a yet earlier publication of some other "*Aster asteroides*," which I have been unable to find, Cronquist's *Aster paternus* is illegitimate and the correct name in *Aster* for this species is the combination by MacMillan.

2. *Sericocarpus linifolius* (L.) B.S.P., *Prelimin. Cat. N.Y. Pl.* 26. 1888. BASIONYM: *Conyza linifolia* L., *Sp. Pl.* 2:861. 1753. **Aster solidagineus*

Michx., [nom. nov.], *Fl. Bor.-amer.* 2:108. 1803. Based on *Conyza linifolia* L. (see Jones & Lowry 1986); not *Aster linifolius* L. 1753. *Sericocarpus solidagineus* (Michx.) Nees, *Gen. Sp. Aster.* 149. 1832.

Galatella obtusifolia Lehm., *Sem. Hort. Bot. Hamburg* 1837 [fide Torr. & Gray 1841].

3. *Sericocarpus oregonensis* Nutt., *Trans. Amer. Philos. Soc.*, ser. 2, 7:302. 1841.

a. *Sericocarpus oregonensis* Nutt. var. *oregonensis*. **Aster oregonensis* (Nutt.) Cronq., *Vasc. Pl. Pacif. Northw.* 5:91. 1955.

b. *Sericocarpus oregonensis* Nutt. var. *californicus* (Durand) Nesom, *comb. nov.* BASIONYM: *Sericocarpus californicus* Durand, *J. Acad. Nat. Sci. Philadelphia*, ser. 2, 3:90. 1855. *Sericocarpus oregonensis* Nutt. subsp. *californicus* (Durand) Ferris, *Contr. Dudley Herb.* 5:100. 1958. *Sericocarpus rigidus* Lindley in W.J. Hook. var. *californicus* (Durand) Blake, *Proc. Amer. Acad. Arts* 51:515. 1916.

4. *Sericocarpus rigidus* Lindley in W.J. Hook., *Fl. Bor.-amer.* 2:14. 1834. **Aster curtus* Cronq. [nom. nov.], *Vasc. Pl. Pacif. Northw.* 5:80. 1955. Based on *Sericocarpus rigidus* Lindley; not *Aster rigidus* L. 1753.

Sericocarpus rigidus Lindley in W.J. Hook. var. *laevicaulis* Nutt., *Trans. Amer. Philos. Soc.*, ser. 2, 7:302. 1841.

Galatella platylepis Nees ex Torr. & Gray, *Fl. N. Amer.* 2:103. 1841 [in syn.].

5. *Sericocarpus tortifolius* (Michx.) Nees, *Gen. Sp. Aster.* 151. 1832. BASIONYM: **Aster tortifolius* Michx., *Fl. Bor.-amer.* 2:109. 1803.

Conyza bifoliatus sensu Walt., *Fl. Carolin.* 204. 1788. Based on *Conyza bifoliatus* L. 1753. *Sericocarpus bifoliatus* (sensu Walt.) Porter, *Mem. Torrey Bot. Club* 5:322. 1894. *Nom. illeg.* *Aster bifoliatus* (sensu Walt.) Ahles, *J. Elisha Mitch. Sci. Soc.* 80:173. 1964. *Nom. illeg.*

Aster collinsii Nutt., *J. Acad. Nat. Sci. Philadelphia* 7:82. 1834. *Sericocarpus collinsii* (Nutt.) Nutt., *Trans. Amer. Philos. Soc.*, ser. 2, 7:302. 1841. *Sericocarpus tortifolius* (Michx.) Nees var. *collinsii* (Nutt.) Torr. & Gray, *Fl. N. Amer.* 2:103. 1841. *Sericocarpus bifoliatus* (sensu Walt.) Porter var. *collinsii* (Nutt.) Blake, *Proc. Amer. Acad. Arts* 51:515. 1916.

Sericocarpus bifolius (sensu Walt.) Porter var. *acutisquamosus* Nash ex Small, *Fl. Southeast. U.S.* 1206. 1903. *Sericocarpus acutisquamosus* (Nash ex Small) Small, *Fl. Southeast. U.S.* 1206. 1903.

As pointed out by Wilbur (1965), it was not Walter's intention to publish a superfluous name but rather to indicate the doubtful identity of the Carolinian plants with the Linnaean species.

Taxa excluded from *Sericocarpus*:

Sericocarpus sipei Henderson = *Aster vialis* (Bradshaw) Blake.

Sericocarpus tomentellus E. Greene = *Aster brickelliioides* E. Greene.

Sericocarpus woodhousei Buckley = *Isocoma pluriflora* (Torr. & Gray) E. Greene.

Jones (1980) included one Asian species, *Aster baccharoides* (Benth.) Steetz, in *Sericocarpus*. This species bears little resemblance to North American *Sericocarpus* but instead apparently is part of the *Aster ageratoides* Turcz. complex in Asia.

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